

Effects of prescribed fire and other plant community restoration treatments on tree mortality, bark beetles, and other saproxylic Coleoptera of longleaf pine, *Pinus palustris* Mill., on the Coastal Plain of Alabama

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Abstract

Treatments to restore understory plant communities of mature (50–80-year old) longleaf pine (*Pinus palustris* Mill.) and reduce risks of wildfire were applied to 10 ha plots that had a substantial shrub layer due to lack of fire. Plots were located in the Coastal Plain of Alabama and treatments consisted of: (1) untreated control, (2) growing season prescribed burn, (3) thin only, (4) thin plus growing season burn, and (5) herbicide plus growing season burn. Thin plus burn plots had significantly higher tree mortality compared to burn only and control plots and, overall, fire was the primary cause of tree death. Most tree mortality occurred within 1-year of treatment. From 2002 to 2004, we captured 75,598 Coleoptera in multiple funnel traps comprising 17 families and 130 species. Abundance of all Coleoptera combined was not different among treatments. Species richness was significantly higher on thin plus burn plots compared to thin only and control plots. Scolytinae (Coleoptera: Curculionidae) were more abundant on thin plus burn plots compared to control plots in fall 2002 but in fall 2003 they were more abundant on thin plus burn, thin only, and herbicide plus burn compared to controls. Among Scolytinae, *Dendroctonus terebrans* (Olivier), *Xyleborinus saxeseni* (Ratzeburg), *Xyleborus* sp. 3, and *Hylastes tenuis* (Eichhoff), showed varying responses to the treatments. Other Curculionidae were significantly more abundant on thin only and herbicide plus burn plots compared to all other treatments in spring 2003 and in spring 2004 they were more abundant on herbicide plus burn plots compared to thin plus burn treatments. Among Cerambycidae, *Xylotrechus sagittatus* (Germar) was higher in abundance in fall 2003 on thin plus burn plots compared to all other treatments except herbicide plus burn plots. Within the predator complex, Trogositidae were higher on thin plus burn plots compared to all other treatments except thin only plots in spring 2003, and Cleridae abundance was higher in spring 2004 on burn only plots compared to all other treatments. Linear regression analyses of dead trees per plot versus various Coleoptera showed captures of Buprestidae, Cerambycidae, Trogositidae, *Acanthocinus nodosus* (Fabricius), *Temnochila virescens* (Fabricius), and *X. saxeseni* increased with increasing number of dead trees. Our results show that the restoration treatments tested did not cause increased bark beetle-related tree mortality and they did not negatively affect populations of early successional saproxylic beetle fauna.

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Keywords: Coarse woody debris; Prescribed fire; Cerambycidae; Trogositidae; Multiple funnel trap; Saproxylic

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests have undergone a dramatic decline since Europeans arrived in North America. Stout and Marion (1993) estimate longleaf pine forests once occupied over 23 million ha. Today longleaf pine occupies less than 5% of its original area (Outcalt and Sheffield, 1996).

Recognition of the problem and development of newer techniques for replanting this species are helping to reverse the trend. However, one prized attribute of longleaf pine forests is the diverse herbaceous understory associated with them when they are frequently burned. Pre-European fire return intervals in Coastal Plain longleaf forests were 2–5 years (Outcalt, 2003). Numerous severe wildfires in the late 1880s and early 1900s resulted in extensive and successful efforts to stop all forest fires. The removal of fire from longleaf forests often results in the development of a thick shrub layer and midstory canopy composed primarily of deciduous hardwood species. The shrub layer combined with the midstory canopy increases the risk of

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catastrophic wildfire and reduces the herbaceous plant community. Therefore, we tested several techniques for their ability to reduce wildfire risk and begin restoring plant and animal communities. One concern was how these treatments would increase tree susceptibility to bark beetles (Coleoptera: Curculionidae: Scolytinae) and how they might affect other early successional saproxylic beetles. Saproxylic invertebrates are dependent, during some part of their life cycle, upon the dead or dying wood of trees (standing or fallen) (Speight, 1989).

Numerous Scolytinae species kill trees and are major forest pests but many others are considered beneficial because they contribute to decomposition and nutrient cycling. The pine bark beetle guild in the southeastern United States includes the southern pine beetle [*Dendroctonus frontalis*] (Zimmermann), black turpentine beetle [*Dendroctonus terebrans*] (Olivier), and three species of engraver beetles [*Ips avulsus* (Eichhoff), *I. grandicollis* (Eichhoff), and *I. calligraphus* (Germar)]. Black turpentine beetle, *Ips* beetles, and the southern pine beetle normally attack *Pinus* spp. that have been weakened or felled, but *Ips* also colonize debris left over from logging operations and black turpentine beetles can be found in stumps (Coulson and Witter, 1984). When populations are high these beetles can attack and kill healthy trees (Coulson and Witter, 1984; Paine et al., 1997). Of the numerous bark and wood boring beetles associated with pines in the southeastern United States, southern pine beetles cause the most tree mortality. *Ips* species are less aggressive and usually attack recently killed, weakened or dying trees. Black turpentine beetles usually attack injured trees or freshly cut stumps and, like southern *Ips* spp., large outbreaks are rare. Tree mortality due to bark beetles results in the loss of millions of dollars each year (Wood, 1982). However, numerous other saproxylic beetles and their associated parasites and predators contribute to overall forest biodiversity and are important for healthy forest ecosystems (Speight, 1989; Grove, 2002).

Other saproxylic beetles, including many other Scolytinae, Cerambycidae, and Buprestidae, have larvae that bore into stems and branches of trees. Most cerambycids and buprestids do not infest logs that have been debarked (Price, 2001), while other beetles, such as Bostrichidae and Anobiidae, can attack dry, debarked logs or wood.

Many other beetles associated with bark beetles are considered beneficial. For example, some members of the Cleridae, Colydiidae, Cucujidae, Histeridae, Nitidulidae, and Trogositidae prey on bark beetles and other wood borers. These predators are considered to be important regulators of bark beetle populations (Schroeder, 1996; Reeve, 1997; Turchin et al., 1999).

Infestations of southern pine beetles usually begin in disturbed areas (lightning, road building, logging, etc.), as well as in areas where dense pine stands exist (Hedden, 1978; Fettig et al., 2007). High stand densities favor southern pine beetle outbreaks because competition for water, space, and sunlight can stress trees resulting in increased susceptibility to beetle attack (Hedden, 1978; Fettig et al., 2007). Once established, southern pine beetles are able to spread quickly in dense pine stands (Bennett, 1968; Hedden and Billings, 1979). Factors affecting southern pine beetle attacks (stand, site, and tree characteristics) differ across physiographic provinces in the

southern U.S. (Belanger et al., 1993) but, in general, the southern pine beetle prefers overmature or weakened trees (Turchin et al., 1999). Southern pine beetles can utilize fire-damaged trees (Cameron and Billings, 1988) but prescribed burns (Dixon et al., 1984; Sullivan et al., 2003) and wildfires (Storey and Merkel, 1960; Hanula et al., 2002) generally do not result in outbreaks when beetle populations are low.

Four treatments were applied to mature longleaf pine stands to reduce their susceptibility to wildfire and to begin restoring the herbaceous understory plant community. In this study we examined their effects on tree mortality and on relative abundance and species richness of bark beetles, some of their beetle predators, and other members of the early successional saproxylic beetle community.

2. Methods

The study site was the Solon Dixon Experimental Forest near Andalusia, Alabama (N 31°9'05" and W 86°41'9"; elevation 45–90 m), which is primarily longleaf pine, with an understory composed mostly of yaupon holly (*Ilex vomitoria* Aiton) up to 2 m tall. Outcalt (2005) provided details on pre-treatment stand conditions.

The experiment was a randomized complete block design consisting of three blocks of five treatments each. Treatments were applied to 10 ha plots and consisted of: (1) untreated control, (2) growing season prescribed burn, (3) thin only, (4) thin plus growing season burn, and (5) herbicide plus growing season burn. Table 1 shows dates treatments were applied.

Table 1
Dates herbicide applications, thinnings, and prescribed burns were applied to 12 plots on the Solon Dixon Experimental Forest, near Andalusia, AL

| Treatment plot ^a | Herbicide | Thinning | Burning |
|-----------------------------|----------------------|---------------|--------------------------------|
| TB | | February 2002 | 5 April 2002 and 28 April 2004 |
| TB | | March 2002 | 22 May 2002 and 4 May 2004 |
| TB | | April 2002 | 1 May 2002 and 29 April 2004 |
| T | | February 2002 | |
| T | | March 2002 | |
| T | | April 2002 | |
| B | | | 23 April 2002 and 6 May 2004 |
| B | | | 21 May 2002 and 6 July 2004 |
| B | | | 15 May 2002 and 15 April 2004 |
| HB | 23–28 September 2002 | | 15 April 2003 |
| HB | 28–30 September 2002 | | 13 May 2003 |
| HB | 1–2 October 2002 | | 16 April 2003 |

^a TB = thin plus burn, T = thin, B = burn, HB = herbicide plus burn.

Thinning removed co-dominant or suppressed trees to produce a residual basal area of 11.5–13.8 m²/ha. Loblolly (*P. taeda* L.), slash (*P. elliotii* Engelm.) and spruce pines (*P. glabra* Walt.), and various hardwoods were specifically targeted for removal. Thin plus burn plots were treated the same as thin only plots but were then burned. Specific details on the prescribed burns can be found in Outcalt (2003) and Kennard et al. (2005). Herbicide plus burn plots received a fall application of 4.5% Garlon 4TM (triclopyr; Dow AgroSciences, Calgary, Alberta) with Timberline 90TM (UAP Timberland, Monticello, AR) surfactant added, and then burned 3 months later. Herbicide was applied using backpack sprayers to target all woody vegetation up to approximately 2 m tall except longleaf pine seedlings and saplings. Growing season prescribed burns were applied to burn only and thin plus burn plots every 2 years during this study, while herbicide plus burn plots were burned only once (Table 1). Several burning techniques, such as back fire, spot fire, and flanking were used on each plot that was burned (Outcalt, 2003). Each plot was marked throughout by grid points spaced 50 m apart to facilitate pre- and post-treatment sampling.

We used 8- and 12-funnel multiple funnel traps (PheroTech International Inc.), and pipe traps developed by Miller (US Forest Service, Athens, GA) to capture saproxylic Coleoptera. Pipe traps were black pipes 1 m in length and 15.2 cm diameter suspended over a collecting funnel (30 cm diameter) and attached cup. Multiple funnel traps are effective for capturing and assessing abundance and diversity of certain forest Coleoptera (Chenier and Philogene, 1989) and pipe traps are effective for Cerambycidae and Curculionidae as well as other beetle species (D. Miller, personal communication). Traps were hung on a nylon string stretched between two trees and one of each trap type was used on each plot. An ultra high release α -pinene packet (Pherotech International Inc.; release rate = 2–5 g/d) and a 95% ethanol packet (release rate = 0.6 g/d) were placed within the 12-unit funnel trap and pipe trap, and a 95% ethanol packet was placed in the 8-unit funnel trap. Collecting cups at the bottom of each trap were partially filled with propylene glycol to preserve captured insects. α -Pinene is a common monoterpene found in the resin of most pine species (Mirov, 1961), whereas ethanol is a general attractant for a variety of bark and wood boring beetles (Fatzinger, 1985; Fatzinger et al., 1987). Traps were placed near the center of each plot 50 m apart and operated for 10 weeks in fall 2002, 10 weeks in spring and fall 2003, and 12 weeks in spring 2004. A 2004 fall sample was not obtained because plots were damaged by hurricane Ivan. Trap samples were gathered and collecting cups refilled with propylene glycol every 3–4 weeks of each trapping period. Samples were stored in 70% ethyl alcohol until identification. We identified beetles to the lowest taxonomic level possible using published keys (Wood, 1982) and reference collections (University of Ga., Natural History Museum; D. Miller, USDA Forest Service, Athens, GA). Those we could not identify were assigned to morphospecies.

Tree mortality surveys were conducted twice per year on each plot. Surveys started December 2001 (before treatments were applied) and continued through March 2004. During mortality surveys we walked along the grid lines looking for

recently killed or dying trees which were then tagged, and the diameter, tree species, cause of death, and types of bark beetles attacking them were recorded. Mortality was attributed to bark beetles if trees responded to attacks with resin flow (Lombardero et al., 2006) or, in the case of black turpentine beetles, attack densities were sufficient to girdle the tree. Only trees that were not tagged and counted in previous surveys were included in the subsequent survey. This resulted in a count of all dead or dying trees per plot that occurred during the previous 6 months. Plots varied somewhat in total area so we divided number of dead trees by number of hectares per plot to calculate number of dead trees per hectare.

PROC GLM (SAS, 1985) was used to conduct two-way ANOVAs with replications and treatments as independent variables, and tree mortality or the various families and species of Coleoptera as dependent variables. We also calculated species richness, Shannon diversity, and evenness. The Ryan–Einot–Gabriel–Welsch multiple range test (REGWQ) was used to compare mean abundances and diversities of Coleoptera among treatments at the $\alpha = 0.05$ level, although we noted where $\alpha < 0.1$ occurred since we were looking for patterns in species responses and felt a less conservative α -value was appropriate (Scheiner and Gurevitch, 2001). Data were tested for normality using the Shapiro–Wilk-W-statistic (PROC UNIVARIATE, SAS, 1985) prior to analysis. Square-root transformation was used to improve normality. Analyses of beetle abundance were run separately for each trapping period since treatments were applied at slightly different times and plots changed with time. To help explain differences in Coleoptera abundance we used the GLM procedure to calculate simple linear regressions of various families and species versus numbers of dead trees per hectare (obtained during tree surveys).

3. Results

Tree mortality was higher in thin plus burn plots compared to burn only, thin only, and control plots ($F_{4,10} = 5.03$, $p \leq 0.02$) (Fig. 1). Herbicide plus burn-treated plots had the second highest tree mortality but the number of dead trees was not significantly different from other treatments. Both thin plus burn- and herbicide plus burn-treated plots had increased tree mortalities after prescribed fire was applied (Fig. 2) and fire was the leading cause of tree death throughout our study (Fig. 3).

We captured 75,598 saproxylic Coleoptera comprising 17 families/subfamilies and 130 species during the 2-year study (Table 2). Overall, total Coleoptera abundance was not significantly different among treatments, but all treated plots had slightly higher numbers than untreated controls (Fig. 4). Species richness was significantly higher on thin plus burn plots compared to thin only and control plots (Fig. 5). Shannon diversity (H') ranged from 2.43 (S.E. = 0.09) to 2.53 (S.E. = 0.03) and evenness (J) from 0.58 (S.E. = 0.02) to 0.62 (S.E. = 0.01) among treatments but these differences were not significant.

A number of Coleoptera families, subfamilies, and species differed in abundance among treatments, but many of these varied in their responses (Table 3). Scolytinae were higher in

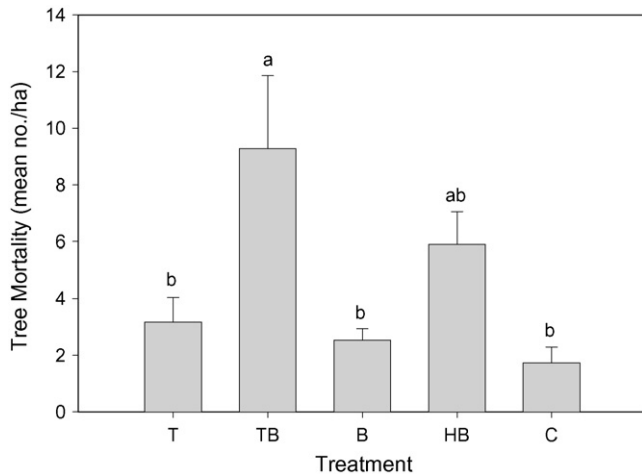


Fig. 1. Mean (\pm S.E.) tree mortality from 2002 to 2004 on all longleaf pine restoration treatment plots on the Solon Dixon Experimental Forest, near Andalusia, AL. Columns with the same letter are not significantly different at $p \leq 0.05$ (REGWQ, SAS, 1985). Treatments were: TB = thin plus burn, T = thin, B = burn, HB = herbicide plus burn, and C = control.

abundance on thin plus burn plots compared to control plots ($F_{4,8} = 3.05$, $p \leq 0.08$) in fall 2002 but in fall 2003 ($F_{4,8} = 4.06$, $p \leq 0.04$) they were more abundant on thin plus burn, thin only, and herbicide plus burn plots compared to controls. Among Scolytinae, *D. terebrans* were more numerous on thin plus burn compared to herbicide plus burn and controls ($F_{4,8} = 5.00$, $p \leq 0.01$) in fall 2002, but by fall 2003 they were higher in abundance on herbicide plus burn plots compared to controls ($F_{4,8} = 3.12$, $p \leq 0.08$). *Xyleborinus saxeseni* (Ratzeburg) were more abundant on thin plus burn plots compared to burn only, herbicide plus burn, and controls ($F_{4,8} = 6.89$, $p \leq 0.01$) in spring 2003 and in spring 2004 they were more abundant on thin plus burn, thin only, and herbicide plus burn plots compared to burn only and control treatments ($F_{4,8} = 15.76$, $p \leq 0.001$).

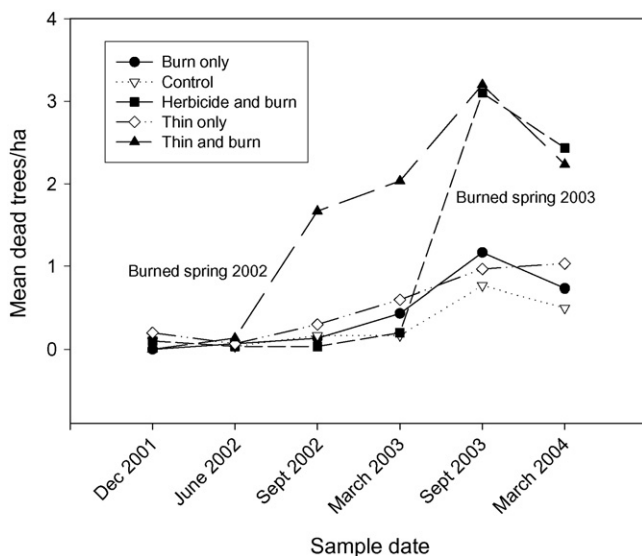


Fig. 2. Mean number of dead pine trees ≥ 10 cm DBH per hectare on fire and fire surrogate treatment plots within each sampling period on the Solon Dixon Experimental Forest, near Andalusia, AL. The December 2001 data were collected before treatments were applied.

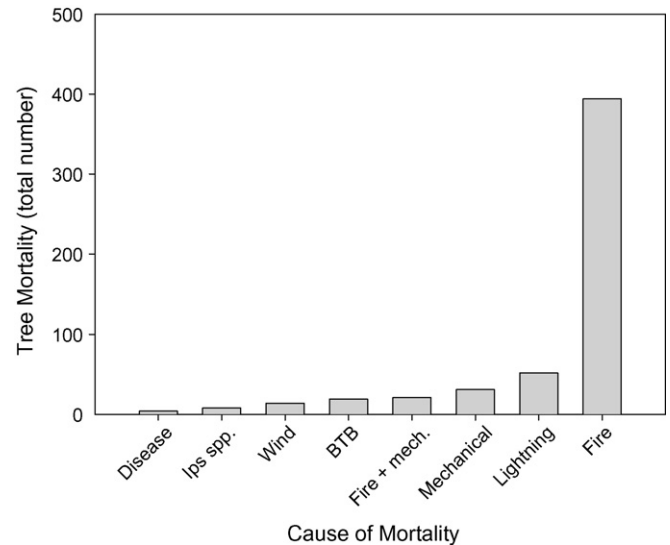


Fig. 3. Total mortality of pine trees ≥ 10 cm DBH and cause of death on restoration treatment plots from 2001 to 2004 on the Solon Dixon Experimental Forest, near Andalusia, AL. Mechanical damage to trees was the result of machinery wounds or old scars from turpentine collection.

Xyleborus sp. 3 were significantly more abundant on thin plus burn and thin only plots compared to all other treatments in spring 2003 ($F_{4,8} = 10.00$, $p \leq 0.003$) and fall 2003 ($F_{4,8} = 6.27$, $p \leq 0.01$), and in spring 2004 they were higher on thin only and burn only plots compared to control treatments ($F_{4,8} = 4.03$, $p \leq 0.04$). In spring 2003, *Hylastes tenuis* Eichhoff were more abundant on herbicide plus burn than they were on thin only or thin plus burn plots ($F_{4,8} = 8.19$, $p \leq 0.01$). However, numbers of *H. tenuis* on control and thin only plots were not significantly different from herbicide plus burn plots.

Curculionidae (excluding Scolytinae) were more abundant on thin only and herbicide plus burn plots compared to all other treatments ($F_{4,8} = 9.67$, $p \leq 0.004$) in spring 2003, and in spring 2004 they were more abundant on herbicide plus burn plots compared to thin plus burn treatments ($F_{4,8} = 3.34$, $p \leq 0.07$). Among the Curculionidae, *Pachylobius picivorus* (Germar) were more abundant in fall 2002 on thin plus burn plots compared to herbicide plus burn and control treatments ($F_{4,8} = 5.10$, $p \leq 0.02$) and in spring 2004 they were more abundant on herbicide plus burn plots compared to other treatments ($F_{4,8} = 3.45$, $p = 0.06$).

Cerambycidae were higher in abundance overall in fall 2003 on thin plus burn plots compared to burn only and control plots ($F_{4,8} = 4.13$, $p \leq 0.04$). Among Cerambycidae, *Xylotrechus sagittatus* (Germar) were higher in fall 2003 on thin plus burn plots compared to all other treatments except herbicide plus burn plots ($F_{4,8} = 3.69$, $p \leq 0.05$). Buprestidae were significantly higher on thin plus burn plots in spring 2004 compared to thin only treatments ($F_{4,8} = 3.61$, $p = 0.06$). Within the saproxylic beetle predator complex, Trogositidae were higher on thin plus burn plots compared to all other treatments except thin only plots ($F_{4,8} = 8.01$, $p \leq 0.007$) in spring 2003.

Linear regression analyses of dead trees per hectare versus various Coleoptera groups showed several positive relationships (Fig. 6). The families Buprestidae, Cerambycidae, and

Table 2

Total numbers of Coleoptera species captured in funnel traps on plots receiving prescribed burns or other longleaf pine restoration treatments on the Solon Dixon Experimental Forest near Andalusia, AL

| Family/subfamily | Genus/species | Total captured |
|------------------|----------------------------------|----------------|
| Anobiidae | <i>Hemicoelus</i> sp. | 39 |
| | sp. 1 | 1 |
| | <i>Trichodesma</i> sp. | 5 |
| Anthribidae | sp. 1 | 33 |
| | sp. 2 | 345 |
| | sp. 3 | 1 |
| | sp. 4 | 1 |
| | sp. 5 | 1 |
| | <i>Toxonotus</i> sp. | 9 |
| Bostrichidae | <i>Amphicerus bicaudatus</i> | 34 |
| | sp. 1 | 2 |
| | sp. 2 | 27 |
| | <i>Xylobiops</i> sp. 1 | 4 |
| | <i>Xylobiops</i> sp. 2 | 22 |
| Buprestidae | <i>Acmaeodera</i> sp. | 2 |
| | <i>Buprestis lineata</i> | 14 |
| | <i>Buprestis maculativentris</i> | 2 |
| | <i>Buprestis salisburyensis</i> | 1 |
| | <i>Buprestis</i> sp. 1 | 20 |
| | <i>Buprestis</i> sp. 2 | 1 |
| | <i>Buprestis</i> sp. 3 | 2 |
| | <i>Chalcophora georgiana</i> | 3 |
| | <i>Chalcophora virginensis</i> | 29 |
| | <i>Chrysobothris</i> sp. 1 | 1 |
| | <i>Chrysobothris</i> sp. 2 | 2 |
| | <i>Chrysobothris</i> sp. 3 | 1 |
| | <i>Chrysobothris</i> sp. 4 | 1 |
| Cerambycidae | <i>Ancylocera bicolor</i> | 7 |
| | <i>Aneflomorpha</i> sp. 1 | 92 |
| | <i>Aneflomorpha</i> sp. 2 | 14 |
| | <i>Aranthocinus nodosus</i> | 142 |
| | <i>Aranthocinus obseletus</i> | 173 |
| | <i>Arhopalus rusticus</i> | 70 |
| | <i>Astylopsis</i> sp. | 1 |
| | <i>Ataxia</i> sp. | 4 |
| | <i>Curius dentatus</i> | 6 |
| | <i>Cyrtophorus</i> sp. | 10 |
| | <i>Cyrtophorus verrucosus</i> | 4 |
| | <i>Eudercus picipes</i> | 1 |
| | <i>Eudercus pini</i> | 1 |
| | <i>Heterachthes</i> sp. | 13 |
| | <i>Knuliana cincta</i> | 47 |
| | <i>Leptostylus</i> sp. 1 | 88 |
| | <i>Leptostylus</i> sp. 2 | 19 |
| | <i>Liopinus</i> sp. 1 | 11 |
| | <i>Liopinus</i> sp. 2 | 2 |
| | <i>Monochamus titillator</i> | 205 |
| | <i>Neoclytus acuminatus</i> | 12 |
| | <i>Neoclytus jouteli</i> | 1 |
| | <i>Neoclytus mucronatus</i> | 16 |
| | <i>Neoclytus</i> sp. | 1 |
| | <i>Obrium</i> sp. | 26 |
| | <i>Parandra</i> sp. | 1 |
| | <i>Parelaphidion</i> sp. | 12 |
| | <i>Prionus</i> sp. 1 | 1 |
| | <i>Prionus</i> sp. 2 | 1 |
| | <i>Rhagium inquisitor</i> | 5 |
| | <i>Saperda</i> sp. | 3 |
| | sp. 1 | 2 |
| | sp. 2 | 10 |
| | <i>Spodylis</i> sp. | 18 |

Table 2 (Continued)

| Family/subfamily | Genus/species | Total captured |
|------------------|----------------------------------|----------------|
| | <i>Stenosphenus</i> sp. | 1 |
| | <i>Stranglia luteicornis</i> | 2 |
| | <i>Strophiona nitens</i> | 2 |
| | <i>Tragidion coquius</i> | 1 |
| | <i>Typocerus zebra</i> | 7 |
| | <i>Xylotrechus sagittatus</i> | 727 |
| | <i>Xylotrechus</i> sp. | 10 |
| Cleridae | <i>Cymatodera</i> sp. | 13 |
| | <i>Enoclerus ichneumoneus</i> | 2 |
| | <i>Neorthopleura thoracica</i> | 1 |
| | <i>Thanasimus dubius</i> | 67 |
| Colydiidae | <i>Colydium</i> sp. | 2 |
| | <i>Pycnomerus</i> sp. | 11,673 |
| Cucujidae | <i>Catogenus</i> sp. 1 | 52 |
| | <i>Catogenus</i> sp. 2 | 3 |
| Curculionidae | <i>Cossonus corticola</i> | 32 |
| | <i>Cryptorhynchus</i> sp. 1 | 31 |
| | <i>Cryptorhynchus</i> sp. 2 | 7 |
| | <i>Curculio</i> sp. | 3 |
| | <i>Dryophthorus</i> sp. | 99 |
| | <i>Hylobius pales</i> | 4019 |
| | <i>Nicentrus</i> sp. | 3 |
| | <i>Pachylobius picivorus</i> | 1413 |
| | <i>Pissodes</i> sp. | 27 |
| | sp. 1 | 1 |
| | sp. 2 | 1 |
| Elateridae | <i>Alaus myops</i> | 392 |
| | <i>Alaus oculatus</i> | 7 |
| | <i>Lacon</i> sp. | 5 |
| | sp. 1 | 1000 |
| Histeridae | <i>Hister</i> sp. | 1 |
| | <i>Platysoma</i> sp. 1 | 31 |
| | sp. 1 | 9 |
| | sp. 2 | 8 |
| | sp. 3 | 1 |
| | sp. 4 | 167 |
| Nitidulidae | <i>Amphotis</i> sp. 1 | 1 |
| | <i>Amphotis</i> sp. 2 | 1 |
| | sp. 1 | 216 |
| Passalidae | <i>Odontotaenius disjunctus</i> | 1 |
| Platypodidae | <i>Platypus flavicornis</i> | 210 |
| Scolytinae | <i>Dendroctonus terebrans</i> | 5947 |
| | <i>Hylastes salebrosus</i> | 10,072 |
| | <i>Hylastes tenuis</i> | 3261 |
| | <i>Hylurgops rugipennis</i> | 1 |
| | <i>Hypotheamus crudiae</i> | 601 |
| | <i>Ips avulsus</i> | 52 |
| | <i>Ips grandicollis</i> | 4392 |
| | sp. 1 | 60 |
| | sp. 2 | 60 |
| | sp. 3 | 396 |
| | sp. 4 | 19 |
| | sp. 5 | 3 |
| | <i>Xyleborinus saxeseni</i> | 9497 |
| | <i>Xyleborus atratus</i> | 28 |
| | <i>Xyleborus</i> sp. 1 | 244 |
| | <i>Xyleborus</i> sp. 2 | 5 |
| | <i>Xyleborus</i> sp. 3 | 1779 |
| | <i>Xylosandrus crassiusculus</i> | 15,723 |
| Tenebrionidae | <i>Alobates pennsylvanica</i> | 1 |
| | <i>Alobates</i> sp. | 2 |
| | <i>Corticeus</i> sp. | 641 |
| | <i>Glyptotus</i> sp. | 4 |
| Trogositidae | <i>Airora</i> sp. | 1 |

Table 2 (Continued)

| Family/subfamily | Genus/species | Total captured |
|------------------|-------------------------------|----------------|
| | <i>Temnochila</i> sp. | 1 |
| | <i>Temnochila virescens</i> | 736 |
| | <i>Tenebriodes collaris</i> | 126 |
| | <i>Tenebriodes marginatus</i> | 4 |
| | <i>Tenebriodes</i> sp. 1 | 39 |
| | <i>Tenebriodes</i> sp. 2 | 32 |

Trogositidae were correlated with dead trees per plot. Species that showed positive relationships with tree mortality were a cerambycid, *Acanthocinus nodosus* (Fabricius), a trogositid, *Temnochila virescens* (Fabricius) and an ambrosia beetle (Scolytinae), *X. saxeseni*.

4. Discussion

Interactions between fire, tree mortality, and bark beetles have been studied extensively in North American coniferous forests (e.g. Miller and Patterson, 1927; Dixon et al., 1984; Ryan and Amman, 1994, 1996; McCullough et al., 1998; Santoro et al., 2001; Bradley and Tueller, 2001; Hanula et al., 2002; Sullivan et al., 2003; McHugh et al., 2003; Wallin et al., 2003; Lombardero et al., 2006; Schwilk et al., 2006). These and other studies show that trees exhibit species-specific responses to fire and that the effects of fire are further complicated by type of fire, fire intensity, season of burning, fire history, and site. In southern pines, most fire-related mortality occurs within the first year after burning (Dixon et al., 1984; Storey and Merkel, 1960; Wade and Johansen, 1986; Hanula et al., 2002) and is related to fire severity as evidenced by bole char height and crown scorch. However, Sullivan et al. (2003) reported tree mortality for several years after burning but could not pinpoint the exact causes.

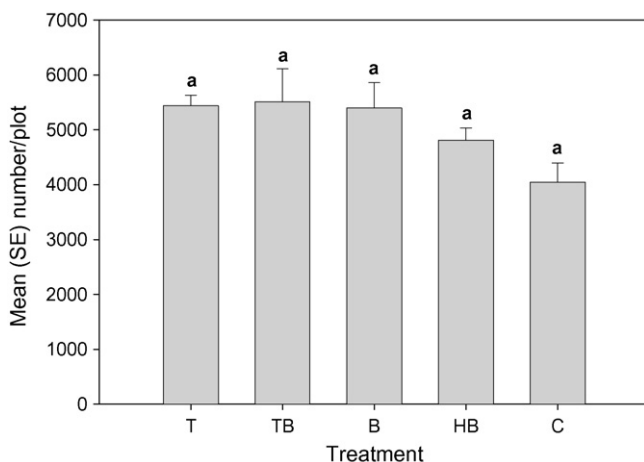


Fig. 4. Mean number (\pm S.E.) of saproxylic Coleoptera captured with multiple funnel traps from fall 2002 to spring 2004 on plots treated with growing season prescribed burns or other longleaf pine restoration treatments on the Solon Dixon Experimental Forest, near Andalusia, AL. Columns with the same letter are not significantly different at $p \leq 0.05$ (REGWQ, SAS, 1985). Treatments were: TB = thin plus burn, T = Thin, B = burn, HB = herbicide plus burn, and C = control.

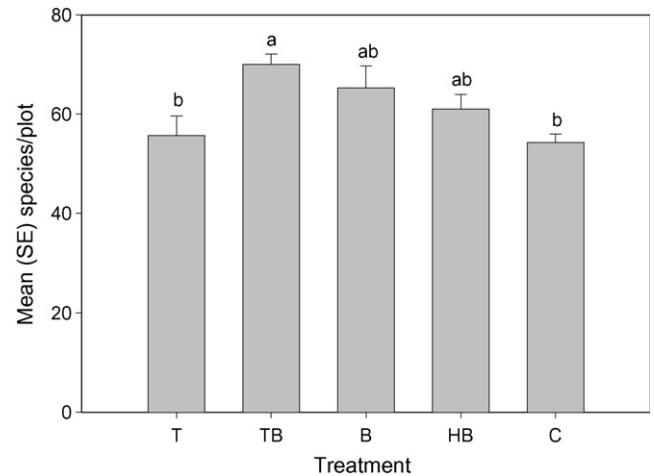


Fig. 5. Mean number (\pm S.E.) of Coleoptera species captured with funnel traps from fall 2002 through spring 2004 on 10 ha plots treated with growing season prescribed burns or other longleaf pine restoration treatments within the Solon Dixon Experimental Forest, near Andalusia, AL. Columns with the same letter are not significantly different ($p \leq 0.05$; REGWQ, SAS, 1985). Treatments were: TB = thin plus burn, M = thin, B = burn, HB = herbicide plus burn, and C = control.

In our study tree mortality peaked within 1 year after burning but additional mortality occurred 2 years after the most severe burns. Although we continued to find some dying trees in the second year after burning, bark beetles did not appear to be the primary cause of mortality. Sullivan et al. (2003) also found no association between bark beetles and extended tree mortality in longleaf pine. Likewise, many studies have shown that bark beetles take advantage of fire-killed trees but none clearly demonstrated bark beetles were responsible for subsequent mortality. Storey and Merkel (1960) attempted to protect fire-damaged trees with insecticides but were late in applying it and unable to completely cover tree boles. Schwilk et al. (2006) noted pitch tubes on tree boles in assessing bark beetle activity following fire, and resin flow might be a good method of assessing post-fire tree condition (Lombardero et al., 2006). We saw very little evidence of pitch tubes and those that were evident were generally black turpentine beetle attacks near wounds created during thinning. Since we saw almost no pitch tubes on fire-damaged trees, but did see bark beetle boring dust, we attributed the mortality to fire damage and not bark beetles. Unlike Santoro et al. (2001), we did not see evidence of increased resin flow following bole scorch.

Tree mortality was higher on plots that were thinned and prescribed burned than on control, thin only or prescribed burn only plots, but thin plus burn plots were not significantly different from herbicide plus prescribed burning treatments. Thin plus burn treatments resulted in a loss of approximately 9 trees/ha compared to normal background levels of 1–2 trees/ha on control plots. This increased mortality was the result of additional fuel loads from logging slash that resulted in hotter fires (Outcalt, 2003). Over 72% of the tree mortality was the result of fire, despite efforts by burning crews to redistribute slash away from the base of trees (Outcalt, 2003), while lightning, the second most common cause of tree mortality,

Table 3
Mean (S.E.) numbers of saproxylic beetles captured with multiple funnel traps on plots receiving growing season prescribed burns or other longleaf pine restoration treatments on the Solon Dixon Experimental Forest near Andalusia, AL

| Family ^a | Genus/species ^a | Treatment ^b | | | | |
|---------------------|----------------------------|------------------------|-----------------|------------------|------------------|------------------|
| | | TB | T | B | HB | C |
| Fall 2002 | | | | | | |
| Buprestidae | | 1.3 (0.3) a | 1.3 (0.3) a | 0.7 (0.7) a | 0.0 (0.0) a | 0.0 (0.0) a |
| Cerambycidae | | 31.3 (1.2) a | 25.7 (10.7) a | 34.3 (5.4) a | 34.7 (6.9) a | 33.0 (10.1) a |
| | <i>A. nodosus</i> | 1.7 (1.7) a | 0.7 (0.3) a | 3.0 (2.5) a | 0.0 (0.0) a | 0.0 (0.0) a |
| | <i>X. sagittatus</i> | 12.3 (3.7) a | 13.7 (6.6) a | 23.3 (7.3) a | 23.7 (3.9) a | 27.7 (7.8) a |
| Cleridae | | 1.7 (0.3) a | 0.3 (0.3) a | 1.3 (0.9) a | 0.3 (0.3) a | 0.3 (0.3) a |
| Colydidae | | 223.3 (85.8) a | 608.3 (259.2) a | 627.7 (276.1) a | 580.0 (85.3) a | 514.0 (73.1) a |
| Curculionidae | | 157.0 (45.7) a | 141.3 (34.9) a | 159.7 (22.0) a | 156.3 (22.6) a | 174.7 (37.0) a |
| | <i>H. pales</i> | 139.7 (45.3) a | 127.0 (31.1) a | 148.0 (19.1) a | 150.0 (23.5) a | 167.3 (36.7) a |
| | <i>P. picivorus</i> ** | 14.3 (2.7) a | 10.0 (1.7) ab | 6.0 (0.6) ab | 5.3 (2.2) b | 4.0 (1.2) b |
| Scolytinae* | | 808.3 (236.7) a | 581.3 (36.4) ab | 496.7 (116.7) ab | 359.7 (26.0) ab | 271.0 (36.4) b |
| | <i>D. terebrans</i> ** | 263.0 (73.1) a | 151.0 (18.9) ab | 150.7 (40.7) ab | 36.0 (8.0) b | 51.3 (10.7) b |
| | <i>H. tenuis</i> | 62.7 (11.1) a | 52.0 (14.2) a | 34.3 (7.2) a | 65.7 (6.8) a | 30.7 (7.3) a |
| | <i>H. salebrosus</i> | 194.0 (54.9) a | 237.3 (40.5) a | 119.7 (38.4) a | 140.7 (23.4) a | 94.0 (22.5) a |
| | <i>I. grandicollis</i> | 22.3 (8.4) a | 8.7 (1.9) a | 16.0 (4.2) a | 17.3 (3.8) a | 13.3 (6.1) a |
| | <i>X. saxeseni</i> | 204.0 (113.7) a | 82.3 (25.6) a | 102.7 (8.2) a | 65.0 (11.6) a | 40.0 (11.1) a |
| | <i>Xyleborus</i> sp. 3 | 5.0 (4.5) a | 0.3 (0.3) a | 2.0 (1.2) a | 2.7 (1.8) a | 2.3 (0.3) a |
| | <i>X. crassiusculus</i> | 30.0 (14.6) a | 13.7 (1.7) a | 28.7 (13.3) a | 11.3 (1.2) a | 18.3 (5.8) a |
| Elateridae | | 2.3 (0.3) a | 4.7 (0.9) a | 2.7 (0.9) a | 2.3 (0.3) a | 1.7 (0.7) a |
| Trogositidae** | | 9.3 (3.5) a | 5.0 (2.0) ab | 9.0 (2.5) a | 0.7 (0.3) b | 2.3 (0.3) ab |
| | <i>T. virescens</i> ** | 5.0 (1.5) a | 3.0 (1.5) ab | 1.7 (0.7) abc | 0.0 (0.0) c | 0.3 (0.3) cb |
| | Spring 2003 | | | | | |
| Buprestidae | | 6.7 (2.3) a | 2.7 (2.2) a | 1.7 (0.9) a | 1.7 (0.3) a | 0.7 (0.3) a |
| Cerambycidae | | 67.0 (20.4) a | 52.0 (20.6) a | 36.3 (11.9) a | 26.7 (3.4) a | 22.7 (8.7) a |
| | <i>A. nodosus</i> | 11.7 (5.8) a | 8.0 (2.3) a | 3.7 (0.9) a | 1.0 (1.0) a | 2.3 (1.2) a |
| | <i>X. sagittatus</i> | 5.0 (2.6) a | 6.0 (4.0) a | 4.0 (1.5) a | 3.3 (1.2) a | 2.7 (1.2) a |
| Cleridae | | 2.0 (0.6) a | 2.0 (1.5) a | 4.0 (1.0) a | 0.7 (0.3) a | 2.3 (1.9) a |
| Colydidae | | 110.3 (12.4) a | 104.0 (28.0) a | 164.7 (22.5) a | 81.3 (16.0) a | 110.7 (30.4) a |
| Curculionidae** | | 57.3 (0.7) c | 95.3 (2.2) ab | 67.3 (3.8) cb | 114.7 (15.6) a | 72.7 (4.3) cb |
| | <i>H. pales</i> | 29.3 (13.0) a | 35.3 (12.1) a | 34.7 (6.4) a | 57.0 (17.1) a | 32.7 (7.0) a |
| | <i>P. picivorus</i> | 24.0 (12.1) a | 55.0 (9.8) a | 30.0 (5.3) a | 54.7 (2.7) a | 37.7 (2.4) a |
| Scolytinae | | 1860.0 (236.7) a | 1767.0 (59.9) a | 1910.7 (66.1) a | 1287.3 (254.0) a | 1357.0 (208.5) a |
| | <i>D. terebrans</i> | 120.7 (32.2) a | 84.7 (19.6) a | 87.7 (22.5) a | 137.0 (58.2) a | 35.7 (10.2) a |
| | <i>H. tenuis</i> ** | 68.7 (19.8) c | 87.7 (21.1) bc | 109.0 (34.9) abc | 164.3 (44.4) a | 145.7 (47.7) ab |
| | <i>H. salebrosus</i> | 298.0 (90.4) a | 373.3 (114.7) a | 287.3 (68.6) a | 300.0 (37.5) a | 298.0 (27.5) a |
| | <i>I. grandicollis</i> | 95.7 (21.2) a | 73.7 (12.9) a | 156.7 (65.9) a | 132.3 (20.1) a | 88.0 (19.6) a |
| | <i>X. saxeseni</i> ** | 479.3 (82.6) a | 371.7 (28.7) ab | 217.3 (15.2) b | 216.7 (53.1) b | 232.0 (15.6) b |
| | <i>Xyleborus</i> sp. 3** | 54.3 (17.3) a | 42.0 (5.3) a | 21.3 (4.4) b | 18.0 (4.5) b | 18.7 (2.8) b |
| | <i>X. crassiusculus</i> | 705.3 (245.0) a | 684.7 (137.4) a | 996.0 (190.7) a | 298.0 (106.8) a | 501.7 (186.7) a |
| Elateridae | | 37.7 (5.7) a | 62.7 (16.8) a | 49.3 (7.1) a | 46.7 (11.7) a | 33.0 (6.8) a |
| Trogositidae** | | 76.7 (13.7) a | 39.0 (6.5) ab | 20.3 (2.6) b | 17.0 (5.5) b | 17.3 (8.4) b |
| | <i>T. virescens</i> ** | 61.3 (9.8) a | 29.7 (4.7) ab | 13.3 (2.4) b | 12.7 (6.4) b | 14.0 (7.9) b |
| | Fall 2003 | | | | | |
| Buprestidae | | 0.3 (0.3) a | 0.3 (0.3) a | 0.0 (0.0) a | 0.0 (0.0) a | 0.0 (0.0) a |
| Cerambycidae** | | 28.0 (7.6) a | 14.0 (4.6) ab | 8.7 (3.7) b | 21.0 (11.9) ab | 10.3 (5.3) b |
| | <i>A. nodosus</i> | 0.0 (0.0) a | 0.7 (0.7) a | 0.7 (0.7) a | 1.0 (0.6) a | 0.0 (0.0) a |
| | <i>X. sagittatus</i> ** | 25.0 (7.8) a | 9.3 (5.6) b | 6.7 (2.7) b | 14.3 (8.4) ab | 9.7 (5.2) b |
| Cleridae | | 2.0 (0.0) a | 2.6 (2.6) a | 4.0 (1.0) a | 0.7 (0.3) a | 2.3 (1.9) a |
| Colydidae | | 125.3 (47.1) a | 105.3 (26.0) a | 157.0 (54.0) a | 74.0 (27.7) a | 80.7 (32.0) a |
| Curculionidae | | 26.7 (12.3) a | 62.7 (7.7) a | 78.0 (31.8) a | 53.7 (5.7) a | 59.7 (7.2) a |
| | <i>H. pales</i> | 23.3 (11.7) a | 58.7 (8.5) a | 74.3 (31.7) a | 44.3 (6.4) a | 57.0 (8.0) a |
| | <i>P. picivorus</i> | 3.0 (0.6) a | 1.7 (0.9) a | 2.3 (0.7) a | 3.7 (2.3) a | 1.7 (0.7) a |
| Scolytinae** | | 361.7 (55.8) a | 371.0 (64.6) a | 222.7 (41.0) ab | 387.3 (49.3) a | 154.3 (37.6) b |
| | <i>D. terebrans</i> * | 88.0 (30.1) ab | 124.3 (60.0) ab | 54.3 (19.6) ab | 211.3 (56.4) a | 34.0 (15.0) b |
| | <i>H. tenuis</i> | 14.0 (4.2) a | 15.0 (7.5) a | 11.3 (1.2) a | 20.0 (5.7) a | 9.7 (2.2) a |
| | <i>H. salebrosus</i> | 47.0 (13.1) a | 59.7 (19.8) a | 53.0 (7.0) a | 67.7 (29.6) a | 22.3 (5.8) a |
| | <i>I. grandicollis</i> | 1.3 (0.7) a | 0.3 (0.3) a | 1.3 (0.9) a | 0.0 (0.0) a | 2.0 (0.6) a |
| | <i>X. saxeseni</i> | 74.7 (20.7) a | 42.3 (22.2) a | 31.7 (11.9) a | 37.7 (10.2) a | 41.7 (6.4) a |
| | <i>Xyleborus</i> sp. 3** | 87.3 (41.1) ab | 90.7 (14.3) a | 46.7 (14.9) abc | 16.0 (6.4) c | 22.0 (12.2) cb |
| | <i>X. crassiusculus</i> | 27.7 (7.4) a | 27.0 (11.5) a | 13.3 (5.8) a | 22.7 (5.5) a | 12.7 (2.0) a |

Table 3 (Continued)

| Family ^a | Genus/species ^a | Treatment ^b | | | | |
|---------------------|----------------------------|------------------------|------------------|----------------|-----------------|-----------------|
| | | TB | T | B | HB | C |
| Elateridae | | 1.0 (0.6) a | 2.0 (1.5) a | 0.7 (0.3) a | 0.7 (0.3) a | 0.3 (0.3) a |
| Trogositidae | | 1.3 (0.7) a | 0.7 (0.3) a | 0.7 (0.3) a | 2.7 (2.2) a | 1.7 (1.2) a |
| | <i>T. virescens</i> | 1.0 (0.6) a | 0.3 (0.3) a | 0.3 (0.3) a | 2.7 (2.2) a | 1.0 (1.0) a |
| Spring 2004 | | | | | | |
| Buprestidae* | | 3.3 (1.3) a | 0.3 (0.3) b | 2.0 (0.6) ab | 2.7 (0.9) ab | 0.7 (0.3) ab |
| Cerambycidae | | 32.3 (5.4) a | 22.7 (7.4) a | 32.0 (5.5) a | 32.3 (6.1) a | 24.7 (4.3) a |
| | <i>A. nodosus</i> | 1.0 (0.6) a | 1.7 (1.7) a | 3.7 (0.7) a | 5.3 (1.2) a | 1.3 (0.9) a |
| | <i>X. sagittatus</i> | 14.3 (6.2) a | 8.3 (3.2) a | 10.3 (3.8) a | 9.7 (2.6) a | 13.0 (4.0) a |
| Cleridae** | | 0.3 (0.3) b | 0.0 (0.0) b | 2.3 (0.3) a | 0.0 (0.0) b | 0.7 (0.3) b |
| Colydidae | | 43.3 (18.4) a | 42.3 (10.4) a | 63.0 (4.5) a | 41.3 (4.1) a | 35.0 (6.8) a |
| Curculionidae** | | 52.0 (4.5) b | 69.7 (7.1) ab | 75.7 (17.8) ab | 125.7 (16.0) a | 78.7 (17.0) ab |
| | <i>H. pales</i> | 6.0 (0.6) a | 29.0 (3.1) a | 34.0 (16.7) a | 47.7 (15.4) a | 44.3 (13.9) a |
| | <i>P. picivorus</i> * | 41.7 (5.4) b | 36.0 (11.4) b | 35.7 (7.8) b | 72.0 (2.6) a | 32.3 (4.7) b |
| Elateridae | | 26.7 (8.4) a | 52.7 (12.2) a | 54.0 (12.1) a | 37.7 (4.4) a | 49.3 (13.1) a |
| Scolytinae | | 1147.3 (121.9) a | 1069.3 (183.8) a | 961.7 (37.0) a | 1173.3 (88.9) a | 832.3 (180.2) a |
| | <i>D. terebrans</i> | 94.7 (45.2) a | 36.0 (14.2) a | 92.3 (12.3) a | 85.7 (7.8) a | 44.0 (15.3) a |
| | <i>H. tenuis</i> | 28.3 (8.0) a | 48.3 (18.8) a | 41.0 (6.0) a | 44.0 (6.7) a | 34.7 (8.4) a |
| | <i>H. salebrosus</i> | 165.3 (69.3) a | 129.0 (45.7) a | 143.3 (19.0) a | 237.0 (67.7) a | 90.7 (49.6) a |
| | <i>I. grandicollis</i> | 182.0 (37.4) a | 163.0 (11.0) a | 150.7 (62.5) a | 175.7 (12.0) a | 163.7 (48.5) a |
| | <i>X. saxeseni</i> ** | 254.0 (75.4) a | 196.3 (24.3) a | 97.3 (16.5) b | 253.3 (37.0) a | 125.7 (17.3) b |
| | <i>Xyleborus</i> sp. 3** | 40.0 (8.7) ab | 49.3 (11.1) a | 44.7 (12.7) a | 19.0 (5.1) ab | 10.7 (2.9) b |
| | <i>X. crassiusculus</i> | 367.7 (33.3) a | 432.0 (93.5) a | 370.7 (46.6) a | 336.0 (14.0) a | 343.7 (136.0) a |
| Trogositidae | | 23.3 (6.1) a | 6.3 (3.4) a | 22.0 (2.6) a | 36.7 (17.8) a | 21.0 (2.9) a |
| | <i>T. virescens</i> | 19.3 (6.7) a | 6.0 (3.6) a | 18.7 (3.3) a | 36.0 (17.5) a | 19.0 (3.5) a |

^a Within each family or genus/species, means followed by the same letter(s) are not significantly different ($p > 0.05$) according to the Ryan–Enoît–Gabriel–Welsch multiple comparison test. Families or genera/species followed with an ** indicates $p \leq 0.05$ and * indicates $p \leq 0.10$.

^b TB = thin plus burn, B = burn, T = thin, HB = herbicide plus burn, C = control.

only accounted for 10% of tree deaths (Fig. 3). Mechanical damage was the result of thinning operations or old wounds caused by previous turpentine operations in some stands we measured. Insects and diseases caused very little direct mortality.

Although fire was the number one cause of death, tree mortality was not uniformly distributed in time (Fig. 2) or space. In fact, one plot experienced much higher mortality than the others and there was considerable variation in tree mortality within the thin plus burn and herbicide plus burn treatments. This can be seen in Fig. 6 where treatment designations are used for each plotted point. Even within plots, high fire intensities resulted in localized pockets of dead trees. This variation in distribution of dead trees within plots, among plots, and over time makes interpretation of beetle abundance and species richness results difficult. Likewise, bark beetles and other deadwood inhabiting Coleoptera occupy a wide range of niches in woody material. In the southeastern United States, little is known about how these beetles respond to alteration of their niche or habitat when trees are fire-scorched or partially burned.

Therefore, it is not surprising that beetle species responded differently to treatments. Overall, saproxylic beetle species richness was higher on thin plus burn-treated plots than on control or thin only treatments. Because thinning alone did not result in higher species richness compared to controls, it appeared prescribed burning was the primary reason for increased species richness. In fact, thin plus burn-treated plots were not significantly richer than other burn treatments. Since burn only plots had significantly fewer dead trees than thin plus

burn plots, the higher species richness we observed is not likely due only to increased volume of large dead wood on those plots. How burning might influence species richness of saproxylic beetles is unclear, but we only measured mortality of pine trees >10 cm DBH. Since fire killed numerous smaller pines, as well as small deciduous hardwood trees, mortality to understory trees and shrubs may explain how fire affected species richness through increased availability of small diameter dead wood.

Total numbers of saproxylic Coleoptera captured in baited multiple funnel and pipe traps were not affected by the various treatments. However, captures of Scolytinae were higher on thin plus burn-treated plots in fall 2002, and on thin plus burn and herbicide plus burn plots in fall 2003. Since the beetles we sampled are dependent on dying or dead trees, these results are consistent with the increased amount of deadwood resulting from those treatments. Examination of Table 3 suggests that the overall effect of these treatments resulted from a general increase in numbers of most Scolytinae species rather than to one dominant species. Although we suspect increased numbers of dead trees on our plots contributed to greater numbers of Scolytinae, only *X. saxeseni* were correlated with increased numbers of dead trees. Reasons for higher numbers of Scolytinae on herbicide plus burn, thin plus burn, and thin only plots in fall 2003 are less clear. Herbicide plus burn plots experienced increased tree mortality following prescribed burns applied in April and May 2003, but thin only plots and thin and burn plots did not. Although fire caused the greatest mortality, thinning created stumps and logging debris for species to breed in. For example, *D. terebrans* numbers were

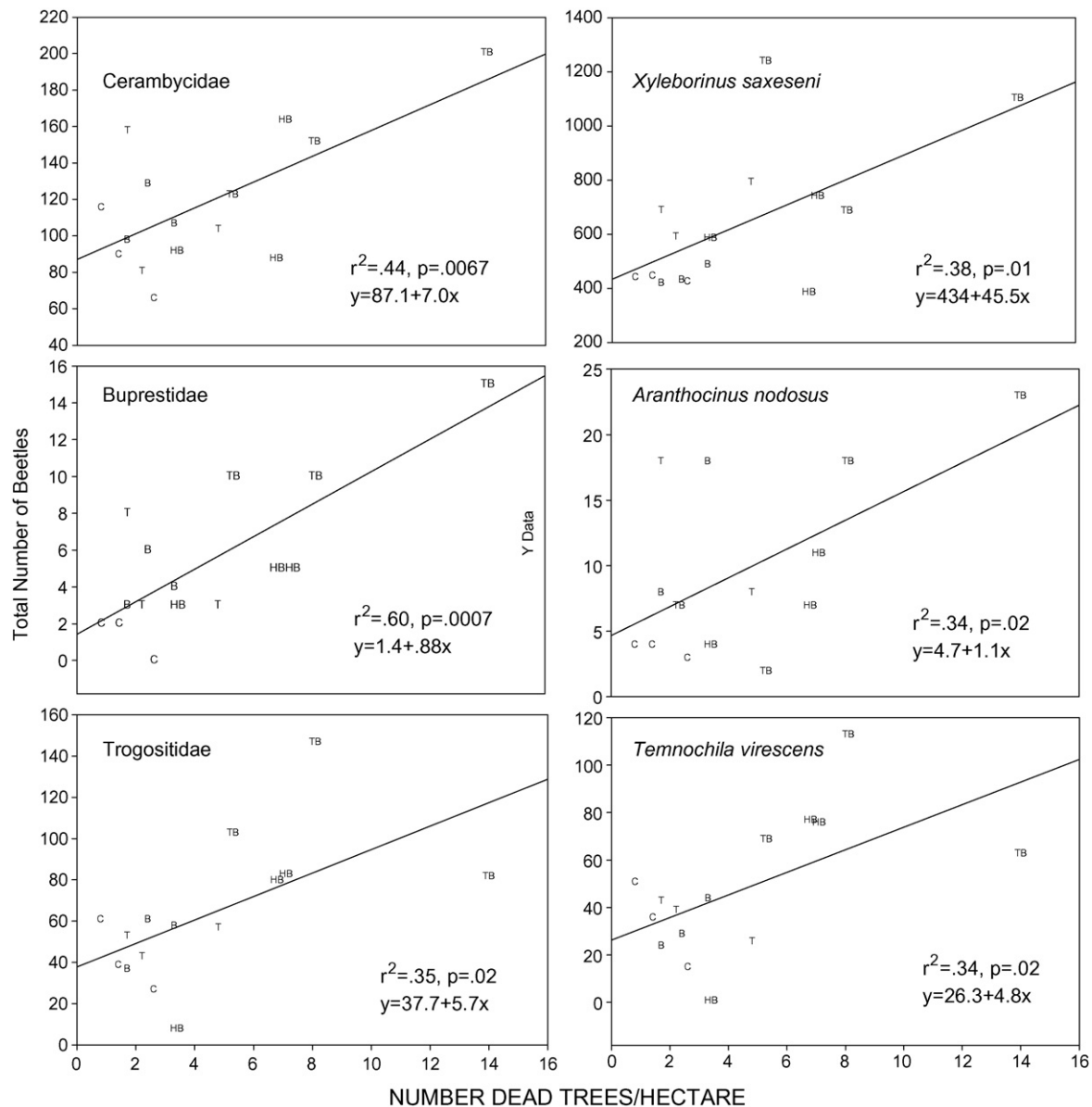


Fig. 6. Linear regression of the number of dead trees per hectare vs. total numbers of various Coleoptera families and species captured in multiple funnel traps on plots receiving growing season prescribed burns or other restoration treatments on the Solon Dixon Experimental Forest. Treatments were: TB = thin plus burn, T = thin, B = burn, HB = herbicide plus burn, and C = control.

highest in fall 2002 and lowest in fall 2003 in thin plus burn plots. Likewise, *H. tenuis* and *H. salebrosus* numbers declined during the same period. Both species utilize pines (USDA Forest Service, 1985) and can be found in stumps and roots. *H. tenuis*, which was found in significantly higher numbers on burn only plots in spring 2003, has been shown to be attracted to burned areas (Sullivan et al., 2003). However, why this species was not more abundant on other plots with burn treatments is unknown.

X. saxeseni was more abundant on thin plus burn plots in spring 2003 and on thin plus burn, thin only, and herbicide plus burn plots in spring 2004. With the exception of the thin only treatment these results appear to be due to increased dead wood, which is supported by the positive correlation between total numbers caught and tree mortality. This beetle feeds on a wide

range of deciduous (Furniss and Johnson, 2002) and coniferous trees (Atkinson and Peck, 1994). Because thinning resulted in a number of small deciduous trees being cut but not removed, thinned plots had an abundance of host material. *X. saxeseni* and *Xylosandrus crassiusculus*, the two most commonly captured Scolytidae comprising 33% of our samples, are both non-native species. Whether they are displacing native saproxylic beetles is uncertain but the large numbers captured raises concerns.

Other economically important Scolytidae, such as *Ips* were not significantly affected by our treatments, which is consistent with the results of Sullivan et al. (2003) and Hanula et al. (2002). However, we captured only one species, *I. grandicollis*, in high numbers. Low captures of other *Ips* species may be due to a bias in the traps. For example, *I. avulsus* (few captured) and

I. calligraphus (none captured) are not attracted to ethanol or turpentine (Billings, 1985; Smith et al., 1993).

More Curculionidae (excluding Scolytinae) were captured on herbicide plus burn plots in spring 2003, when the plots were burned. Among Curculionidae, *P. picivorus* were captured in higher numbers on thin plus burn plots and herbicide plus burn plots in fall 2002 and spring 2004, respectively. Adult weevils deposit eggs within freshly cut pine stumps or roots of recently killed trees and larvae feed beneath the bark. Hotter fires and higher tree mortality associated with thin plus burn and herbicide plus burn plots probably attracted weevils in search of oviposition sites. These weevils are attracted to areas severely burned by wildfire (Hanula et al., 2002) or high severity prescribed fires (Sullivan et al., 2003), and to areas thinned and later burned (Fox and Hill, 1973).

Cerambycidae were caught in high numbers throughout the study but only in fall 2003 were differences significant due to high numbers of *X. sagittatus*. Most Cerambycidae captured, including *X. sagittatus*, feed on dead and dying trees. Cerambycids would be expected to increase in areas with high numbers of dead trees through attraction from outside and subsequent emergence following brood development. We found cerambycid abundance was positively correlated with numbers of dead trees.

Many predators of bark beetles follow their prey (Vité and Williamson, 1970). Higher numbers of Trogositidae on thin plus burn and thin only plots in fall 2002, and on thin plus burn plots in spring 2003, were most likely due to an increase in their bark beetle prey. These predators were positively correlated with numbers of dead trees where higher numbers of their prey live, but why they did not follow similar trends during other trapping periods (when prey was also high) is unknown.

5. Conclusion

The forest management practices we evaluated can result in initially higher tree mortality and more wood-dwelling Coleoptera. Fire was the primary cause of mortality in this study. Of the species capable of killing trees, only black turpentine beetles increased in abundance but the increase did not result in significant tree mortality. None of the treatments tested resulted in increased mortality from other bark beetles. Our results show that treatments such as thinning followed by prescribed burning or herbicide treatment of shrubs followed by burning did not increase longleaf pine susceptibility to bark beetle attack and they benefited some early successional saproxylic beetle species.

Our results varied depending on treatment, season, and species, which demonstrates that no one treatment or timing of treatments provides all the needed habitat for saproxylic beetles. Most genera or species with significant increases in abundance were on one of the treated plots, primarily the thin plus burn and herbicide plus burn treatments which had higher tree mortalities. None of the treatments resulted in a reduction in saproxylic beetle populations. This study focused on early successional species and it is unlikely that higher abundances of these early colonizing saproxylic beetles would continue to be

found on treated plots compared to untreated controls as the amount of newly created dead wood decreases over time. Future research should focus on long-term changes among saproxylic Coleoptera assemblages and the impacts of non-native species.

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